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Footprints pull origin and diversification of dinosaur stem-lineage deep into Early Triassic

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Summary: The ascent of dinosaurs in the Triassic is an exemplary evolutionary radiation, but the earliest phase of dinosaur history remains poorly understood. Body fossils of close dinosaur relatives are rare, but indicate that the dinosaur stem lineage (Dinosauromorpha) originated by the latest Anisian (ca. 242-244 Ma). Here we report footprints from the Early–Middle Triassic of Poland, stratigraphically well constrained and identified using a conservative synapomorphy-based approach, which shift the origin of the dinosaur stem lineage back to the early Olenekian (ca. 249-251 Ma), approximately 5-9 million years earlier than indicated by body fossils, earlier than demonstrated by previous footprint records, and just a few million years after the Permian/Triassic mass extinction (252.3 Ma).

Dinosauromorph tracks are rare in all Polish assemblages, suggesting that these animals were minor faunal components. The oldest tracks are quadrupedal, a morphology uncommon among the earliest dinosauromorph body fossils, but bipedality and moderately large body size had arisen by the early Anisian (ca. 246 Ma). Integrating trace fossils and body fossils demonstrates that the rise of dinosaurs was a drawn-out affair, perhaps initiated during recovery from the Permo-Triassic extinction.

Keywords: Dinosauria; Dinosauromorpha; Triassic; evolutionary radiation; mass extinction; ichnology

1. INTRODUCTION

The tempo of the Triassic dinosaur radiation is central to longstanding debates about dinosaurian success, Triassic mass extinctions, and the establishment of “modern” ecosystems [1-5]. The earliest phase of this radiation, following the divergence of the dinosaur stem lineage (Dinosauromorpha, which includes all taxa closer to dinosaurs than to the other main archosaur clades, pterosaurs and crocodylomorphs), is poorly understood. Attention has primarily focused on the body fossils of approximately 10 basal dinosauromorph taxa on the stem lineage towards dinosaurs, which are some of the rarest discoveries in the Triassic terrestrial record [6-11]. Furthermore, because of the sister-taxon relationship between dinosauromorphs and pterosaurs [12-14], which are first known from the Late Triassic, ghost lineages cannot currently bear on the timing or pace of dinosauromorph origins, despite indicating an Early Triassic origin for archosaurs more broadly [15-16]. Surprisingly, footprints are an often ignored source of data in this debate, although trace fossils are often more abundant than body fossils, may be preserved in environments not conducive to the preservation of bone, and can provide direct evidence of behaviour and habitat preferences [17].

Footprints of possible early members of the dinosaur stem lineage have been reported from several sites around the world [18-22], and many have been described as substantially predating dinosauromorph body fossils [e.g. 19], which are first known from the Middle Triassic (?latest Anisian, ca. 242-244 Ma: 11). However, many of these interpretations are controversial due to poor preservation [23] and uncertain age and stratigraphic correlations [18, 24], and because a rigorous synapomorphy-based approach for identifying track makers and differentiating potential dinosauromorph prints from those of other reptiles is infrequently used [19, 25, 26]. As a result, footprints are often ignored or largely dismissed by workers

focusing on body fossils [4, 5, 27, 28], and are rarely marshaled as evidence in macroevolutionary studies of the dinosaur radiation [1-3]. In effect, the early dinosauromorph footprint record has been marginalized and is yet to be fully integrated with the body fossil record.

Recent discoveries have placed the Polish Triassic record as a key to understanding the ascent of dinosaurs. The most complete, well preserved, and locally abundant body fossils of a basal dinosauromorph are from the middle-late Carnian of Silesia [8, 29]. Body fossils and abundant footprints of early dinosaurs are present in the Carnian, Norian and Rhaetian of Poland [30, 31]. Here, we report three well dated Early and Middle Triassic footprint assemblages from the Holy Cross Mountains of central Poland that contain unequivocal dinosauromorph tracks (Figs 1, 2), identified by possession of synapomorphies seen in dinosauromorph skeletons [19, 25, 26]. Such synapomorphy-based identifications have long been difficult due to the rarity of dinosauromorph body fossils [19, 26], but new skeletal discoveries now make it possible to compare dinosauromorph hindlimbs and footprints in great detail [8, 10, 11]. Furthermore, pinning an accurate age on many Triassic fossil sites is difficult, but the central European location of the Polish tracksites allows for direct correlation with classic Triassic sections in the Germanic Basin. Therefore, the new Polish finds, identified using synapomorphies and reliably dated, provide new and direct constraints on the tempo of the early dinosauromorph radiation.

2. DESCRIPTION

(a) Stryczowice tracksite

The first tracksite, Stryczowice, contains a diverse assemblage of tetrapod footprints, including rare tracks of the small (maximum track length 40 mm) basal dinosauromorph

ichnogenus *Prorotodactylus*. *Prorotodactylus* possesses synapomorphies of several nested clades, including Archosauria (narrow-gauge trackways, with a pace angulation of approximately 130°) and Dinosauromorpha (bunched metatarsus, digitigrade prints with lack of metatarsal imprints, reduction of digits I and V, posterior deflection of digit V: ref. 26; note that some of these features may be optimized as synapomorphies of the slightly more inclusive Avemetatarsalia, the “bird-line” archosaur clade that includes dinosauromorphs and pterosaurs). Among dinosauromorphs, *Prorotodactylus* possesses synapomorphies of the peculiar genus *Lagerpeton* (digit IV longest in foot, progressive decrease of digits IV-III-II, digit III angled relative to midline: ref. 6). Therefore, these prints can be attributed to a quadrupedal basal dinosauromorph closely related to *Lagerpeton*.

Furthermore, the tracks exhibit two important features that corroborate their referral to a *Lagerpeton*-like dinosauromorph and differentiate them from other common Triassic taxa and ichnotaxa. First, the three central digits are essentially parallel, with interdigital angles less than 10° on average, and in those rare, very deep pes imprints that preserve traces of the metatarsals, all metatarsal pads are united and form a single, compact unit (Fig. 2I). Second, the posterior margin of the footprint is straight, which is indicative of a bunched metatarsus and foot acting as a single structure, instead of a series of splayed digits, as shown by biomechanical simulations [32]. A bunched metatarsus is a synapomorphy of Avemetatarsalia [12, 14], and the nearly parallel central digits are unique to *Lagerpeton*, in which the digits barely diverge from each other because the distal articular surfaces are approximately in line and not splayed as in other taxa [6].

Other Triassic ichnotaxa, such as *Rhynchosauroides*, which is superficially similar to *Prorotodactylus*, have more splayed central digits (25-40° interdigital angles) and curved posterior margins [33; electronic supplementary material]. In addition, these tracks also lack other synapomorphies of Archosauria, Avemetatarsalia, and Dinosauromorpha, including

narrow-gauge trackways and digitigrade posture (Fig. S6 and electronic supplementary material). Importantly, the parallel central digits and straight posterior margin are seen in all specimens of *Prorotodactylus*, regardless of substrate (Fig. 2F-I), and are absent on *Rhynchosauroides* tracks preserved on the same slabs (Fig. S6), indicating that they are not artifacts of preservation but rather reflect genuine morphological features of the trackmaker.

Biostratigraphic information, including new palynomorph and conchostrachan data, and lithostratigraphic correlations indicate a Smithian (early Olenekian) age for the Stryczowice site (electronic supplementary material), which is correlative with the lower Middle Buntsandstein and stratigraphically below all sites in the Germanic basin that preserve dinosauromorph tracks (*Rotodactylus*: refs. 19, 24). These Polish tracks are thus the oldest known evidence of the dinosauromorph lineage.

(b) *Wióry tracksite*

The second tracksite, Wióry, was previously described briefly [33, 34], but lacked a well constrained age and its ichnofossils have yet to be grounded in an explicit synapomorphy-based assessment. New biostratigraphic and magnetostratigraphic information (electronic supplementary material) indicates an early Spathian (early late Olenekian) age for the Wióry site, which preserves rare imprints of *Prorotodactylus*. These are identified as a *Lagerpeton*-like dinosauromorph based on the same characters discussed above. All tracks are quadrupedal, and no other dinosauromorph ichnogenera are present. Increased sampling since the initial report of Ptaszyński [33] shows that *Prorotodactylus* was a rare component of the ichnofauna (Fig. 1).

(c) *Baranów tracksite*

The third tracksite, Baranów, is dated as latest Olenekian–early Anisian (electronic supplementary material), based on palynomorph and conchostrachan biostratigraphy. It is correlated to the Röt Formation, a characteristic Buntsandstein unit of the Germanic Basin, based on lithostratigraphy and biostratigraphy. This site has yielded two dinosauromorph ichnogenera.

The first, *Rotodactylus*, is common in the latest Olenekian–Ladinian worldwide [18, 19, 20, 24], and has previously been identified as a *Lagerpeton*-like basal dinosauromorph [35]. A synapomorphy-based assessment corroborates this identification, as first outlined by Haubold [19], as these tracks possess unequivocal features of avemetatarsalians or dinosauromorphs such as digitigrade posture and a reduction of digits I and V (see electronic supplementary material). As with other *Rotodactylus* tracks, the Polish prints are similar to *Prorotodactylus*, but differ in that the fifth digit is fully rotated posteriorly [18, 19]. All Polish *Rotodactylus* tracks are small, with none measuring greater than 50 mm in length.

We have identified nine specimens of a new, larger (120–140 mm) ichnospecies from Baranów, *Sphingopus* isp., which is the rarest ichnotaxon in the assemblage (electronic supplementary information). These tracks clearly belong to Archosauria, based on the narrow gauge trackways, and Dinosauroomorpha, based on all of the synapomorphies elucidated above for *Prorotodactylus*. The lack of associated manus imprints and high pace angulation (178°) indicates that the track maker was walking bipedally, and these prints therefore represent the oldest known bipedal dinosauromorph trackways [19]. Strangely, digit V is functional, a morphology hitherto unknown in dinosauromorph tracks or body fossils. However, digit V is directed about 15° posterolaterally relative to digits II–IV, unlike the nearly perpendicular deflection in chirotheroid tracks, which are attributed to crocodile-line archosaurs [35] and differentiated from dinosauromorphs by lack of the latter group's synapomorphies. Overall, *Sphingopus* isp. matches most closely in morphology and size the

feet of *Herrerasaurus* [36] although some differences occur in the morphology and position of digit V (electronic supplementary material). The nearly tridactyl morphology, with digit III as the longest, indicates that *Sphingopus* isp. corresponds to a dinosauromorph more derived than *Lagerpeton*, and therefore closer to the ancestry of true dinosaurs, possibly theropods [22, 26].

3. DISCUSSION

(a) *Preservation and systematic affinities of the tracks*

Associating a particular footprint with a trackmaker is often difficult, but using synapomorphies to assign footprints to explicit clades is the most reliable and defensible method [25, 26]. Even this, however, can be problematic, since footprints represent the interaction of soft tissues of the foot with the substrate. Soft tissues are rarely fossilized and difficult to reconstruct with certainty, and different substrates and preservational styles may cause differences in footprint shape wholly unrelated to the morphology of the trackmaker. With this in mind, it is significant that, regardless of substrate type and preservation, the Polish tracks invariably preserve archosaur and dinosauromorph synapomorphies, including features such as narrow gauge trackways, digitigrade posture, and reduction of the peripheral digits that should register in tracks regardless of the nuances of soft tissue morphology. They are often found alongside other tracks, such as *Rhynchosauroides*, that do not preserve these characters. Therefore, the archosaur and dinosauromorph affinities of the Polish tracks are secure.

(b) *Early-Middle Triassic dinosauromorph faunal abundance*

Dinosauriomorph footprints are remarkably rare in the Wióry and Baranów assemblages, and comprise no more than 2 and 3%, respectively, of total vertebrate tracks discovered at those sites (electronic supplementary material). Changes in absolute abundance through time are important features to document during evolutionary radiations [1, 3], but the scarcity of Early-Middle Triassic terrestrial body fossils has left open the question of basal dinosauriomorph abundance. In both Polish assemblages dinosauriomorph footprints are exceptionally rare relative to chirotheroid tracks, attributed to crurotarsans (crocodile-line archosaurs), supporting an emerging view that the latter group was more pre-eminent than the dinosaur line throughout most of the Triassic [2]. Strikingly, however, dinosauriomorph tracks at Stryczowice and Wióry, although rare overall, are preserved in considerable abundance as localized, monospecific assemblages, similar to a younger site in the Germanic basin that is dominated by *Rotodactylus* tracks [19, 24]. The abundance of tracks preserved in these bedding planes may reflect increased activity, rather than a large number of individuals; similarly, rare prints may reflect decreased activity. In any case, it is clear that basal dinosauriomorphs were not uniformly common or active in Early-Middle Triassic faunas.

(c) Postural and body size evolution in dinosauriomorphs

The Polish tracks help document the transition from quadrupedality to bipedality, and from small to large size, in the dinosaur lineage. Bipedality is often considered a synapomorphy of dinosauriomorphs (sometimes equivocally) [26, 27], and was historically heralded as a “key character” explaining the ascendancy of dinosaurs over other Triassic reptile groups [37]. However, postural evolution on the line to dinosaurs has been difficult to assess because the forelimb morphology of most basal dinosauriomorphs is unknown.

Because of this uncertainty, footprints are crucially important, and tracks of *Prorotodactylus* and *Rotodactylus* indicate that at least some basal dinosauriomorphs were

quadrupedal, but with pedal overstep of the manus suggesting that the forelimb was much reduced relative to the hindlimb [19, 33]. Bipedal posture was achieved by at least one lineage by the early Anisian, judging from the bipedal Baranów *Sphingopus* isp. tracks. In concert with this change, the size of the largest dinosauromorph footprints increases substantially between the Stryczowice/Wióry and Baranów sites. However, the large, bipedal tracks are rare in the Baranów ichnoassemblage, and are outnumbered more than 3:1 by quadrupedal dinosauromorph tracks.

Along with the recent discovery of the quadrupedal basal dinosauromorphs *Silesaurus* [8] and *Asilisaurus* [11], the Polish tracks raise the questions of whether bipedality may have arisen multiple times on the line to dinosaurs, and of which postural and locomotor condition was ancestral for Dinosauria itself. These questions are currently difficult to address with body fossils and footprints, but future discoveries and integration of both types of data should shed light on this contentious issue.

(d) *Early-Middle Triassic dinosauromorph habitats*

One principal advantage of footprints is that they are often found in different facies and environments than body fossils and cannot be transported, thereby providing precise information on habitat preferences [17, 25]. The Polish footprints, and those of the European Buntsandstein in general [19], were formed on the floodplains of large meandering rivers, far inland from the coast. Such environments are not conducive to preserving fragile bones of small, basal dinosauromorphs. Early members of the dinosaur stem-lineage frequented such environments in the Early-Middle Triassic of Europe, and this may have been a more general preference.

(e) *Revised timeline of early dinosauromorph history*

The Polish footprints prompt a substantial extension of early dinosaur history (Fig. 3). The dinosauromorph lineage originated by at least the early Olenekian, within a few million years of the devastating Permo-Triassic mass extinction (PTE). The narrowing gap between the extinction and the oldest stem dinosaurs raises the intriguing possibility that the dinosauromorph radiation may have been part of the general recovery from the PTE, not an unrelated event that occurred 10-20 million years later as previously considered [38]. Although pre-extinction diversity and ecosystem complexity were slow to recover [38], major tetrapod clades may have arisen in the immediate aftermath of the PTE [16, 39]. This hypothesis, however, clearly demands further study.

Moderately large size and bipedal posture among dinosauromorphs are first known in the latest Olenekian-early Anisian, and tracks that may belong to true dinosaurs are present in the Ladinian of Europe [20] and South America [21]. The first dinosaur body fossils are known from near the Carnian-Norian boundary [4, 5, 40], but only in the Norian did dinosaurs diversify into the range of shapes and sizes (morphological disparity) characteristic of their post-Triassic history [2]. Finally, after the Triassic-Jurassic transition, dinosaurs experienced a burst of diversification (lineage splitting: ref. 41) and became the dominant mid-to-large size terrestrial vertebrates in ecosystems worldwide [1, 27].

In sum, the dinosaur radiation was a drawn-out affair, unexplainable by broad platitudes, with perhaps 40-50 million years separating the earliest basal dinosauromorphs from the first faunas entirely dominated by dinosaurs. This story has mostly been pieced together with rare bones, but a long overdue synthesis of the body fossil record with often neglected data from footprints, grounded in a rigorous stratigraphic and synapomorphy-based assessment, may provide a new frontier in understanding the evolution of early dinosaurs.

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Figure 1. Stratigraphic positions, frequencies, and maximum sizes of dinosauromorph tracks and tetrapod track assemblages in the generalized lithological profile of the Buntsandstein (Early-Middle Triassic) of the Holy Cross Mountains, Poland (for details see electronic supplementary material, figs S2, S3, S4).

Figure 2. Dinosauromorph tracks from the Early and Middle Triassic of the Holy Cross Mountains, southern Poland. A–E. *Prorotodactylus* isp. from the early Olenekian of Stryczowice. F–K. *Prorotodactylus mirus* Ptaszyński 2000 from the late Olenekian of Wióry. L–O. *Sphingopus* isp. from the early Anisian of Baranów. P. *Sphingopus* isp. Trackway (from Baranów) composed of three imprints (l and m designate specimens L and M). Scale bars: A–K, 1 cm; L–P, 10 cm; M–O, 5 cm.

Figure 3. A general timeline for early dinosaur history, from the split of the dinosaur stem-lineage from other archosaurs during the Early Triassic until the Early Jurassic. Footprints, including specimens described herein, document the earliest phase of this radiation, and extend the dinosaur stem-lineage and constituent groups earlier in the Triassic than indicated by body fossils (see also supplementary online material, fig. S9). The transition from quadrupedality to bipedality, along with an increase in absolute faunal abundance and body size, are captured by Triassic footprint assemblages. The ascent of dinosaurs was a drawn-out process that unfolded over nearly the entire Triassic and Early Jurassic. Timescale based upon ref. 42. Silhouettes courtesy of C. Abraczinskas, F. Ippolito, P. Sereno.